THE OCCURRENCE OF *TETRAGONIA DECUMBENS* AND *TRACHYANDRA DIVARICATA* IN SOUTHERN AUSTRALIA.

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ABSTRACT

Tetragonia decumbens (Aizoaceae) and *Trachyandra divaricata* (Liliaceae *s.l.*) are native to southwestern Africa. They are coastal dune plants and have similar distributions, not only in Africa, but also in Australia. Herbarium specimens, published records and fieldwork have been used to document their history in Australia. Most early records are from the vicinity of ports and this suggests that propagules arrived with ships' ballast or cargo. Experiments have shown that the fruits of *Tetragonia decumbens* are buoyant; some stay afloat for more than two years and are still viable. *Trachyandra divaricata* is a tumbleweed: its 'crown' of mature flower stalks is easily dislodged and, blown about by wind, drops numerous small seeds from the fruit capsules. The seeds are not buoyant, but dry flower stalks float for several weeks. The different dispersal characteristics of the two species correlate with occupation of somewhat different niches in the dunes: *Tetragonia decumbens* on strandlines and unstable dunes, *Trachyandra divaricata* on more densely vegetated dunes. These characteristics are also implicated in the manner in which the species have enlarged their ranges: the herbarium records appear to support the thesis that offshore currents are a prime agent in the regional dispersal of *Tetragonia decumbens* and that cars, boats and planting stock have greatly contributed to that of *Trachyandra divaricata*.

INTRODUCTION

Tetragonia decumbens Miller (Aizoaceae), Sea Spinach and *Trachyandra divaricata* (Jacq.) Kunze (Liliaceae *s.l.*: Asphodeliaceae), Dune Onion Weed or Strapweed are native to southwestern Africa. They are coastal dune plants and occur from the arid coast of Namibia to the Port Elizabeth region on the southern coast of the Republic of South Africa (Figure 1). Throughout this range *Tetragonia decumbens* forms an important element of the dune flora. Along the dry coasts of the Namib it is one of the few species that stabilizes small, isolated hummock dunes, while further to the south, in the Cape Region, where the beach daisy *Arctotheca populifolia* forms characteristic hummock dunes, *Tetragonia decumbens* often occurs in dense patches, especially in hollows or blowouts. Along the southern coast, where *Tetragonia*

decumbens reaches its eastern limit, it is still abundant, but native grasses become more important (Lubke *et al.* 1997). *Trachyandra divaricata*, from what I have been able to ascertain from the literature (Obermeyer 1962, Van der Maarel 1993), is of lesser importance in the dune vegetation and, although present in pioneer associations, it is more common in stable communities.

Both species have been introduced to Australia and at present have a similar distribution (Figure 1). In southwestern Western Australia they have become familiar elements of the dune flora (Smith 1985, Hussey *et al.* 1997) and it is difficult to imagine that it is only 70 years ago that the first herbarium collections of these species were made near Cottesloe. However, this was not the first time that they gained a foothold in Australia as earlier occurrences have been documented from Victoria and, for *Tetragonia decumbens*, New South Wales. Later, also *Trachyandra divaricata* found its way to New South Wales and both species appeared in South Australia.

In this paper I aim to answer three questions. Firstly, how did they arrive in Australia; secondly, how did they spread; and thirdly, what is the likelihood that they will spread further?

PLANT HABIT AND PROPAGULE CHARACTERISTICS

Tetragonia decumbens is a perennial herb, although older stems become quite woody. As indicated by the specific epithet, its stems spread over the ground or over obstacles such as flotsam timber or sand-stilling fences. The stems grow several meters long and produce shoots from the leaf axils. The yellow flowers

Figure 1. The geographic distribution of *Tetragonia decumbens* and *Trachyandra divaricata* in relation to climate. The maps of Africa and Australia south of 26° S have been overlaid for easy comparison of the climates of the coastal regions, which have been classified according to Köppen's scheme (after Schulze and McGee 1978 and Gentilli 1972, respectively). BS: semi-arid, and BW: arid climates with mean annual temperatures above (h) or below 18°C (k); Cs: 'Mediterranean' climates with winter rains and hot, dry summers (a) or long, mild summers (b); Cf: humid mild-winter climates with appreciable rainfall throughout the year, either with hot summers (a), or with mild summers (b).

are borne in the leaf axils of these shoots, each on a short stalk, in number varying from one to four per axil. Petals are lacking; the colour results from the calyx lobes as well as the stamens, which ripen before the stigmas spread out. The calyx has four ridges, which grow out to broad, corky wings in the fruit. This characteristic gives the fruits buoyancy, and although incapable of lifting the fruits into the air, the wings enlarge the surface area and, hence, fruits can be blown over the ground in strong winds. Fruit size varies in length between 10 and 14 mm and in width between 12 and 19 mm, the up to 7 mm broad wings included.

Trachyandra divaricata plants form large rosettes of drooping, long, strap-like leaves which grow from an irregularly shaped rootstock (Heyligers 1999a). These rosettes develop a 'crown' of leafless, branched inflorescences, about 70 cm long. The flowers are pale lilac and much sought after by honeybees. Each inflorescence produces about 200 capsules, each containing on average 11 seeds. Thus, the crown of a well-developed plant may have produced in the order of 50 000 seeds by the end of the flowering period. These seeds are pyramidal, 2 mm across, and unadorned. Dried-off 'crowns' are torn away by wind and function as tumbleweeds. The inflorescence stems are filled with aerenchyma and are buoyant when dry.

MATERIAL AND METHODS

To determine buoyancy, fruits of *Tetragonia decumbens* and seeds and dry inflorescences of *Trachyandra divaricata* were put in containers with seawater. The viability of fruits and seeds was tested at the start of these experiments and at various intervals afterwards. For this they were placed in petri dishes lined with moist filter paper after rinsing with fresh water.

Specimen label details were obtained from state and university herbaria as specified in the Acknowledgments. This information was supplemented by published records and, over the last 25 years, by field observations along many sections of sandy coastline south of the Tropic of Capricorn.

As on previous occasions, I have used these data to infer mode of introduction and subsequent spread based on the presumption that the earliest collections would have come from the area where the species first became naturalized and that this area served as the focus of further dispersal. For strandline and foredune species with buoyant propagules this has lead to the supposition that the dispersal of such species happens through making 'leaps' entrained in major current systems with subsequent filling in of the 'gaps' by means of largely wind-driven along-shore drift (Heyligers 1983, 1989, 1991, 1993, 1996, 1999a). However, as Keighery and Dodd (1997) have shown for the spread of *Euphorbia paralias* along the west coast of Western Australia, 'leaps' can also be achieved by other means such as transport on boats.

RESULTS

A) Buoyancy and seed viability

Most *Tetragonia decumbens* fruits sank within the first few weeks, but some remained buoyant for more than two years and still contained viable seed. The viability of seeds in sunken fruits decreases over time; some seeds still germinated after 15 months, but none did after two years.

The seeds of *Trachyandra divaricata* sank

within minutes, but dry flower stalks stayed afloat for several weeks and some for up to a month and a half. They sank once they became waterlogged. Out on the beach, many seeds will drop before the sea is reached and later during drifting at sea, thus diminishing the colonization potential of a stranded bunch. Some sunken seeds kept in seawater were still viable after eight months.

B) History of discovery and spread

Western Australia (Figure 2)

In August 1932, both *Tetragonia decumbens* and *Trachyandra divaricata* were collected at Cottesloe. From there they spread to become a common element in the foredune vegetation along the west coast between Perth and Cape Leeuwin and have also been reported from several offshore islands

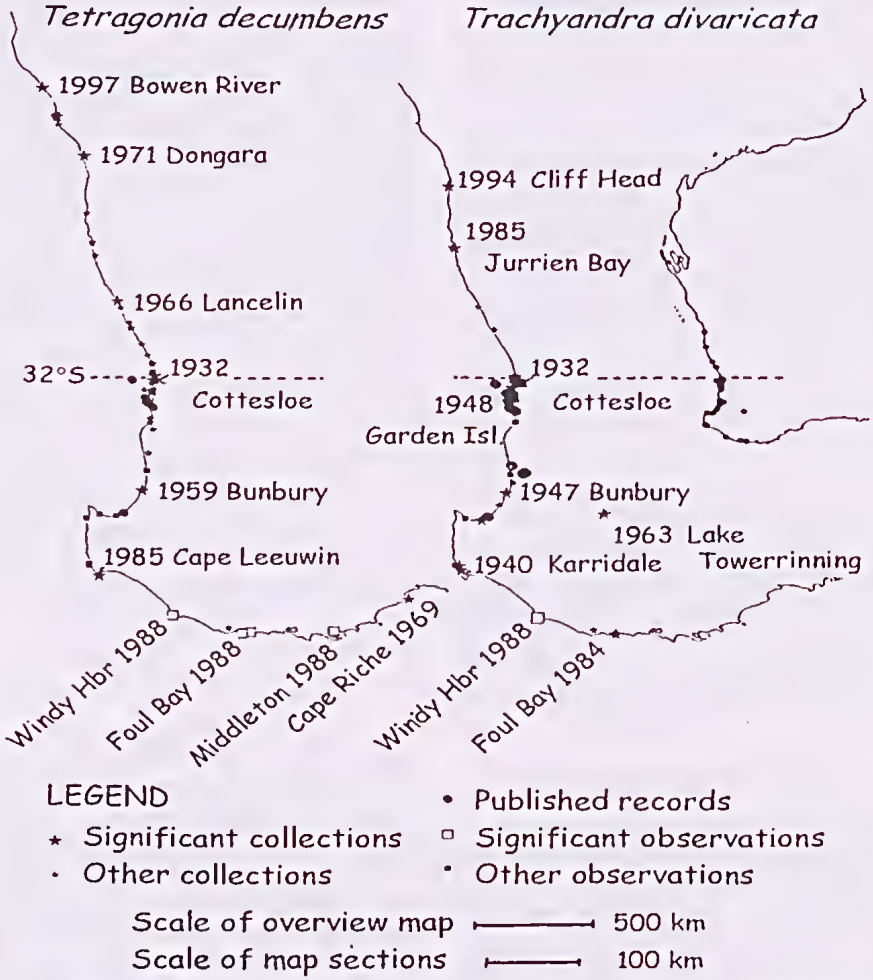

Figure 2. Documented occurrences of *Tetragonia decumbens* and *Trachyandra divaricata* in southwestern Western Australia.

(Creed and Bailey 1998, Keighery 1998, McArthur 1957, Rippey *et al.* 1998, Sauer 1965, Storr 1962). Both species have been collected further to the north, *Tetragonia decumbens* earlier and more often than *Trachyandra divaricata*. They have also spread along the southern coast. *Tetragonia decumbens* occurrences are still sporadic (pers. obs.), but *Trachyandra divaricata* is reported to be widespread as far as Albany (Hussey *et al.* 1997).

On the coastal plain south of Perth *Trachyandra divaricata* has spread inland and in times of drought, when other feed has become scarce, it has been eaten by livestock, sometimes with lethal consequences (Huxtable *et al.* 1987). In 1963 *Trachyandra divaricata* was also collected at Lake Towerrinning, 110 km inland from the coast as the crow flies, but only 25 km west of the highway between Perth and Albany.

Victoria (Figure 3)

Between 1908 and 1913 both species were collected at Coode Island, the ballast ground for Port Melbourne (Tovey 1911). However, they did not persist (Willis 1970, 1972), nor is there any evidence that they spread along the shores of Port Phillip Bay.

New South Wales (Figure 3)

In 1916 *Tetragonia decumbens* was found

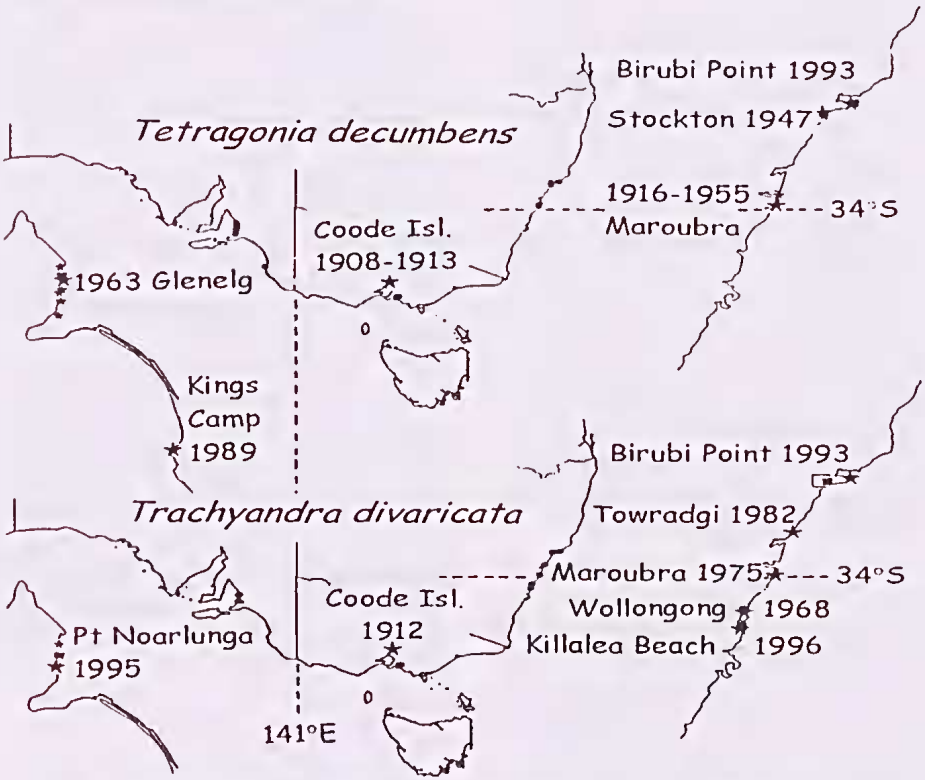

Figure 3. Documented occurrences of *Tetragonia decumbens* and *Trachyandra divaricata* in southeastern Australia. For legend and scales see Figure 2.

in Sydney at Maroubra beach and judged to 'be a welcome addition to the dune flora in the capacity of a sandbinder' (Hamilton 1917). In 1919 it was also collected at Camp Cove, just inside the entrance to Port Jackson. At the time the plants were incorrectly identified as *Tetragonia nigrescens*, a mistake that has only recently been recognized (Heyligers 1999b). The species has in the mean time disappeared from the Sydney foreshores, although at Maroubra it persisted at least until 1955.

In 1947 *Tetragonia decumbens* was collected at Stockton, former ballast ground for Port Hunter. The species still persists on the restored dune terrace, where by 1994 *Trachyandra divaricata* had become established as well. In 1993 both species were collected in a restored dune area at Birubi Point which forms the northeastern end of Stockton Beach, but in 1998 I could only find *Tetragonia decumbens* at that location. Earlier, in 1968, *Trachyandra divaricata* had already been found on the restored foredunes at Fairy Meadows near Wollongong. It is still common there and has turned up at several other dune rehabilitation sites on the Central Coast of New South Wales. A frequently planted shrub at these sites is *Acacia saligna*, a widespread coastal species indigenous to Western Australia and often used for dune stabilization overseas (Marchant *et al.* 1987).

South Australia (Figure 3)

Tetragonia decumbens has been known to occur in the Adelaide region since 1963, when it was collected at Glenelg. Over the years it has been found at scattered locations, mostly in disturbed habitats such as the boulder scree of sea walls, or near parking areas for beachgoers. In a dune restoration area at Hallett Cove it forms low hummocks. Where it occurs it grows well, but it does not appear to be aggressively spreading.

In 1989 I found a single *Tetragonia decumbens* plant on the foredune between Kings Camp and Cape Jaffa among other introduced dune species common in the area, e.g. *Cakile maritima*, *Euphorbia paralias* and *Thinopyrum junceum*. Ten years later it was still there and had grown considerably, but no offspring was spotted in the vicinity.

The first record of *Trachyandra divaricata* from South Australia is from Tumby Bay (Hewson 1987): in 1964 a single plant was found near the schoolyard and promptly eradicated. However, an annotation with the specimen (Alcock C35; AD) mentions that a revision of the identification in 1987 led to the conclusion that it was not *Trachyandra divaricata*, but probably a species of *Asphodelus*.

In the early 1990s true *Trachyandra divaricata* was discovered on beaches of Port Adelaide, where it has become locally common. The only other known locality in the state is some 40 km further to the south, at Port Noarlunga, where a small population occurs in a dune swale. Extensive dunecare activities are carried out in the dunes, largely concentrating on combating *Arctotis stoechadifolia*. In the midst of the area with *Trachyandra divaricata* flourished one large sprawling female *Spinifex longifolius* tussock! This species is indigenous to the northern and western coasts of continental Australia (Heyligers 1988).

DISCUSSION

A) How did they arrive?

All early collections of *Tetragonia*

decumbens and *Trachyandra divaricata* were made near major ports, providing strong circumstantial evidence that propagules of these species came in with ballast or cargo taken aboard in Cape Town. The contemporary collections at Coode Island as well as the later ones at Cottesloe suggest that on both occasions the propagules arrived in the same 'contaminated' load.

Later collections in southeastern Australia, namely those of *Trachyandra divaricata* in New South Wales and of both species in the Adelaide region, often come from locations where dune restoration works have been carried out. In the Wollongong area and at several other locations in New South Wales the occurrence of *Trachyandra divaricata* is strongly linked with the presence of *Acacia saligna* and hence it is quite likely that *Trachyandra divaricata* was introduced with *Acacia saligna* planting stock obtained from Western Australia. The evidence for the source of propagules in the Adelaide area is less clear. The occurrence of a single *Spinifex longifolius* plant at Noarlunga makes one wonder whether at some stage materials from Western Australian origin have been used during dune restoration projects.

The occurrence of a single *Tetragonia decumbens* plant at Cape Jaffa is an intriguing one. It is not unlikely that the fruit from which this plant grew drifted in from Western Australia. I base this on an analogous case, namely the colonization of the dunes between Robe and Beachport by the Western Australian strain of *Arctotheca populifolia* in the 1980s (H. Lee pers. comm., author's obs.). The nearest although sporadic occurrences of this species are along the shores of the Great Australian Bight and are presumed to have established through long-distance dispersal on ocean currents passing the coast of southwestern Western Australia (Heyligers 1983). However, the possibility remains that the fruit arrived in the area as a stowaway as the plant grows within sight of the fishing settlement of Kings Camp.

B) How did they spread?

As both species are most common in Western Australia, the data from that State are the more suitable ones for trying to reconstruct how their present range was attained. The earlier *Tetragonia decumbens* records, with the exception of the collection at Cape Riche, show a steady progression of dates towards the north and south from Perth. I assert that this pattern is the result of fruits from established populations being carried by offshore currents to outlying locations. Local dispersal, filling in gaps left between newly established populations, would be effected by inshore currents as well as by wind.

The data for *Trachyandra divaricata* reveal a different pattern. Soon after the initial collections in the Perth area, this species was found near Karridale, 300 km further south. Subsequently it became established on the dunes in the intervening area and spread to paddocks inland. One may assume that the these areas were readily colonized through tumbleweed action and, coupled with the fact that seeds appear to grow best in disturbed situations, through dune rehabilitation activities.

In 1963 *Trachyandra divaricata* turned up at Lake Towerrinning, well away from its natural habitat and since the 1980s it has been found at several outlying coastal locations, all of which are popular fishing spots. Hence I suspect that hitch-hiking on cars, boats and trailers has been the way the seeds were dispersed to these places.

Occurrences in New South Wales and South Australia have remained localized. Human activities appear to have been the main agent for dispersal to new locations.

C) Will they spread further?

Climate-wise, there are obvious parallels between the southern coastal regions of Africa and Australia, although the configuration of the Australian coastline leads to a duplication of the Mediterranean conditions in southwestern Western Australia and south-eastern South Australia (Figure 1). In Africa the distribution of both *Tetragonia decumbens* and *Trachyandra divaricata* is centred on the area with a Mediterranean climate in the southwest. To the north it extends into areas with desert climates; towards the south it stretches into the area with a climatic regime transitional to the summer rainfall region of the southeast. In view of this broad climatic tolerance, and given that other environmental conditions are suitable, it may be assumed that in time both species will continue to enlarge their range in Australia as far as climatic conditions allow. Hence, we can expect range expansion along much of the sandy shores along the west coast, the Great Australian Bight and the Gulfs of South Australia.

The reason for the disappearance of *Tetragonia decumbens* and *Trachyandra divaricata* from Coode Island is not known. It would be my guess that it was due to a change in the inherently ephemeral habitat conditions of a ballast ground. Occurrences of both species in New South Wales could possibly remain localized due to unsuitable climatic conditions, especially the higher rainfall during the summer months. As *Trachyandra divaricata* in particular appears to spread through human activities and in Western Australia has proliferated on subcoastal sandy soils where it has led to livestock poisoning, an attempt should be made to eradicate occurrences in New South Wales. I would like to recommend a similar action for *Trachyandra divaricata* occurrences in the Adelaide area, although because of the more favourable growing conditions, it would have to be soon, before spread has gone much further. *Tetragonia decumbens* appears to be less aggressive and I do not anticipate that a similar action is warranted for this species. It could even be useful as a sand stabilizer in the drier areas.

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REFERENCES

CREED, K.E. and BAILEY, M. 1998. Decline in migratory waders at Pelican Point, Swan River, Western Australia. *The Stilt* 33: 10–14.

GENTILLI, J. 1972. *Australian Climate Patterns*. Nelson, Melbourne.

HAMILTON, A. A. 1917. Topographical, ecological, and taxonomic notes on the ocean shoreline vegetation of the Port Jackson District. *Journal of the Royal Society of New South Wales* 51: 287–355.

HEWSON, H. J. 1987. *Trachyandra*. *Flora of Australia*. 45: 234–236.

HEYLIGERS, P.C. 1983. An appraisal of the beach daisy (*Arctotheca populifolia*) with a view to its possible use for dune stabilization. *Victorian Naturalist* 100: 48–54.

HEYLIGERS, P.C. 1988. 'Spinifex' L.: setting the record straight. *Australian Systematic Botany Society Newsletter* 56: 13–15

HEYLIGERS, P.C. 1989. Sea spurge (*Euphorbia paralias*), a strandline pioneer new to the Perth region. *Western Australian Naturalist* 18: 1–6.

HEYLIGERS, P.C. 1991. History in the making: naturalized strandplants down-under. Joint symposium of the Australian Systematic Botany Society and the New Zealand Botanical Society, Auckland, New Zealand, 25-27 November 1991. Abstracts.

HEYLIGERS, P.C. 1993. Dispersal of *Euphorbia paralias* in southern Australia. 1993 Open Forum and Symposium Conference of the Ecological Society of Australia, Australian National University, Canberra. Abstracts.

HEYLIGERS, P.C. 1996. Rockets down under: what's going on? 1996 Open Forum and Symposium Conference of the Ecological Society of Australia, James Cook University, Townsville. Abstracts: 47

HEYLIGERS, P. C. 1999a. Dispersal of the exotic coastal dune plants *Gladiolus gueinzii* and *Trachyandra divaricata* in Australia. *Cunninghamia* 6: 315–29.

HEYLIGERS, P. C. 1999b. The occurence and history of *Tetragonia decumbens* (Aizoaceae) in New South Wales. *Telopea* 8: 371–73.

HUSSEY, B.M.J., KEIGHERY, G.J., COUSENS, R.D., DODD, J. and LLOYD, S.G. 1997. *Western Weeds; a guide to the weeds of Western Australia*. Plant Protection Society of Western Australia (Inc.), Victoria Park, WA.

HUXTABLE, C.R., CHAPMAN, H.M., MAIN, D.C., VASS, D., PEARSE, B.H.G. and HILBERT, B.J. 1987. Neurological disease and lipofuscinosis in horses and sheep grazing *Trachyandra divaricata* (branched onion weed) in south Western Australia. *Australian Veterinary Journal* 64: 105–108.

KEIGHERY, G.J. 1998. The weeds of Garden Island – an annotated list. *Western Australian Naturalist* 22: 61–76.

KEIGHERY, G.J. and DODD, J. 1997. Occurrence and spread of Sea Spurge (*Euphorbia paralias*) along the west coast of Western Australia. *Nuytsia* 11: 285–286.

LUBKE, R.A., DAVIS, A.M., STEINKE, T.D. and BOUCHER, C.

1997. Coastal Vegetation. Pp 300–321 in: Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds.): *Vegetation of Southern Africa*. Cambridge University Press, Cambridge, U.K.

MCARTHUR, W.M. 1957. Plant ecology of the coastal islands near Fremantle, W.A. *Journal of the Royal Society of Western Australia* 40: 46–64.

MARCHANT, N.G., WHEELER, J.R., RYE, B.L., BENNETT, E.M., LANDER, N.S. and MACFARLANE, T.D. 1987. *Flora of the Perth Region*. Western Australian Herbarium, Department of Agriculture, Western Australia.

OBERMEYER, A.A. 1962. A revision of the South African species of *Anthericum*, *Chlorophyton* and *Trachyandra*. *Bothalia* 7: 669–767.

RIPPEY, E., RIPPEY, J, DUNLOP, N., DURANT, C. GREEN, B. and LORD, J. 1998. The changing flora of the Shoalwater Bay islands. *Western Australian Naturalist* 22: 81–103.

SAUER, J. 1965. Geographic reconnaiscance of Western Australian seashore vegetation. *Australian Journal of Botany* 13: 39–69.

SCHULZE, R.E. and MCGEE, O.S. 1978. Climatic indices and classifications in relation to biogeography of southern Africa. Pp. 19–52 in Werger, M.J.A. (Ed.) *Monographiae Biologicae* Vol. 31: *Biogeography and Ecology of Southern Africa*. Junk, The Hague.

SMITH, G.G. 1985. *A guide to the coastal flora of south-western Australia*. Handbook No. 10 (2nd edition). Western Australian Naturalists' Club, Perth.

STORR, G.M. 1962. Annotated flora of Rottnest Island, Western Australia. *Western Australian Naturalist* 8: 109–124.

TOVEY, J.R. 1911. Some notes on Coode Island and its flora. *Victorian Naturalist* 28: 57–61.

VAN DER MAAREL, E. (ed.) 1993. Dry Coastal Ecosystems – Africa, America, Asia and Oceania. *Ecosystems of the World*. 2B. Elsevier, Amsterdam.

WILLIS, J.H. 1970. *A Handbook to Plants in Victoria*, Vol. I, second edition. Melbourne University Press, Carlton, Vic.

WILLIS, J.H. 1972. *A Handbook to Plants in Victoria*, Vol. II. Melbourne University Press, Carlton, Vic.